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Ecological aspects of aggregation in Collembola

BY

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INTRODUCTION

Several systems have been given for ecological classification of soil animals (CHRISTIANSEN, 1964). For Collembola an important system has been developed by GISIN (1943). This classification is fundamentally a morphological one, but seems to be very well associated with the ecology of these animals.

In this system an interesting development is indicated within the group of Collembola from euedaphic soil-inhabitants via hemiedaphic litter-dwelling species to atmobiotic species, living in the vegetation. This development is owed to an increasing drought resistance, which in extreme cases is realized in the formation of a simple tracheal system (i.e. *Sminthuridae*). It looks like as if incapacity to resist drought has been the most important threshold, which prevented the development of the variability in life-forms existing in the higher groups of insects.

The relation between drought resistance and variability of life-habits is subject of these investigations. It is studied in surface dwelling Collembola, as these seem to have made progress in this development.

The species are compared in their humidity requirements; their locomotory reactions in different humidity conditions are studied and their activity and inactivity phenomena in field conditions are analysed. On the basis of the investigated relationships, the ecological aspects of this behaviour can be discussed.

MATERIALS AND METHODS

The collembolan species : *Tomocerus minor* (Lubbock), *Lepidocyrtus cyaneus* Tullberg, *Orchesella cincta* (Linné), *Entomobrya nivalis* (Linné), *Isotomurus palustris* (Müller) and *Isotoma viridis* Bourlet were sampled in a

Pinus sylvestris plantation at Schiermonnikoog, one of the Dutch Wadden Islands, where also the field data were obtained.

The humidity requirements were established by preference experiments in humidity gradients and by means of resistance experiments in different relative humidities (JOOSSE, 1970). In the same conditions the locomotory activity was studied (JOOSSE & GROEN, 1970).

Activity phenomena in relation to reproduction were studied in animals which were synchronized in their reproduction by means of a starvation of 7 days in 20° C (JOOSSE & VELTKAMP, 1970).

RESULTS

1. Humidity requirements

a. *Preference experiments.*

A clear difference could be observed in the preferences of the individual species (Fig. 1). *Tomocerus minor, Isotoma viridis* and *Lepidocyrtus cyaneus* seem to be most sensitive for high humidities. *Lepidocyrtus* shows a pronounced choice, revealing a stenohygric nature. *Orchesella* has a broad preference indicating an euryhygric nature. *Entomobrya nivalis* seems to be adapted to somewhat dryer conditions, since it prefers a lower value in the gradient.

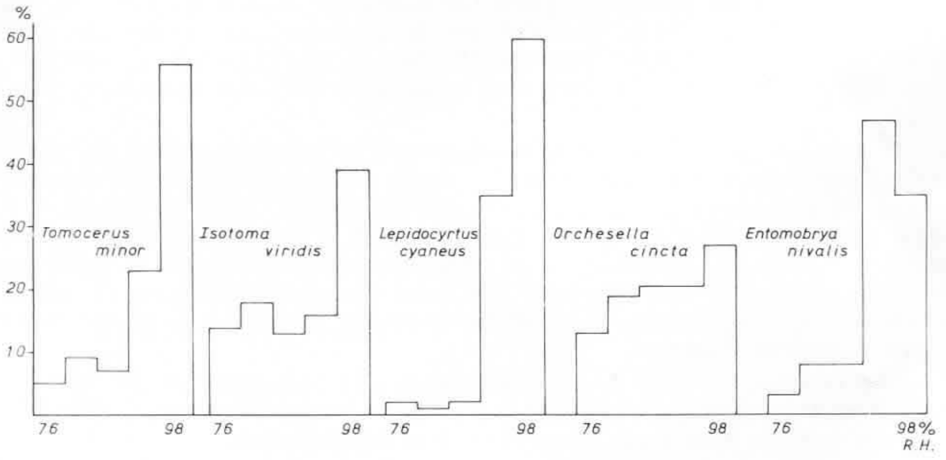

FIG. 1. — Frequency-histograms of the humidity preferences of Collembola.

b. *Resistance experiments.*

The LD50 points, obtained in 20° C, 60 % R.H. conditions are given in Table I.

TABLE I

LD_{50} of Collembola in 20° C, 60 % R. H. conditions

	LD_{50} in minutes
Tomocerus minor	35
Lepidocyrtus cyaneus	335
Orchesella cincta	365
Entomobrya nivalis	570
Isotoma viridis	40

It is obvious that *Tomocerus minor* is the most sensitive to desiccation, immediately followed by *Isotoma viridis.* The other species are much more resistant in the sequence *Lepidocyrtus, Orchesella, Entomobrya,* which supports the results on the preferences of the species.

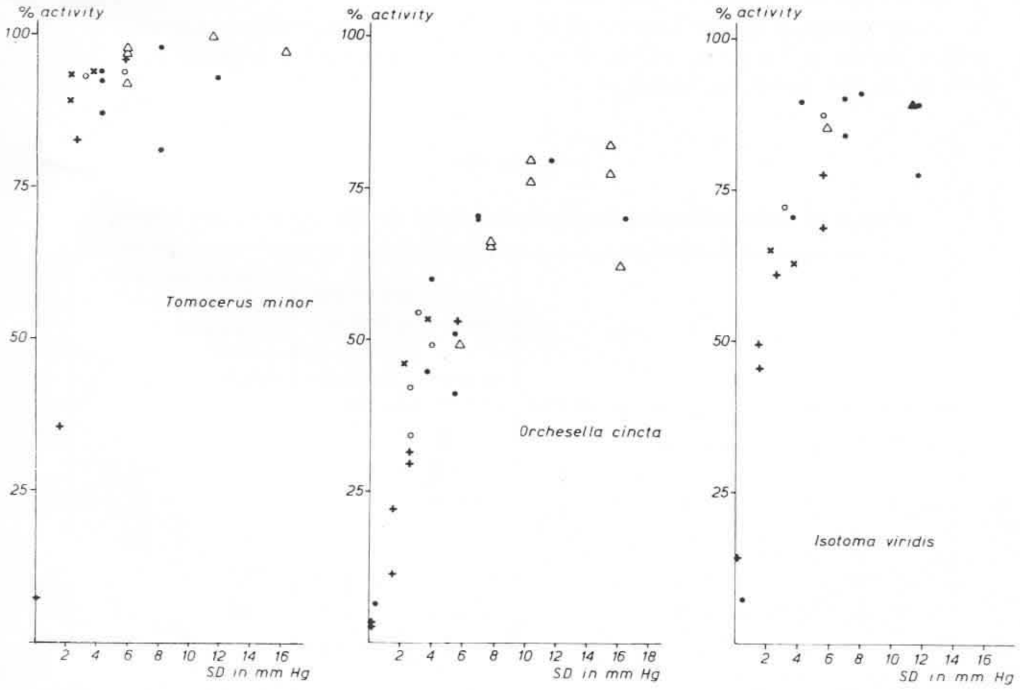

FIG. 2. — Locomotory activity in relation to saturation deficit. Each point represents the data of 100 specimens. The s. d. values are obtained at different temperatures:
△ = 25°, ● = 20°, o = 15°, × = 10°, + = 5° C.

2. Locomotory reactions in different humidity conditions

The locomotory reactions were studied by establishing the percentage of active animals (of 100 individuals), placed in different saturation deficit (s.d.) values. The data of 3 species are shown in Fig. 2. It is clear that with increasing s.d. an increasing activity can be noticed, levelling off at higher s.d. values, which appeared to be lethal. The more sensitive the species are, the more intensive is their reaction to a changed s.d.

3. Inactivity phenomena in the field

The frequency distribution of the number of Collembola in soil cores, suggests that the Collembola occur in aggregations. Aggregation can be expressed by means of the relation between s^2 (variance) and m (mean) in: $s^2 = am^b$ (LEWIS & TAYLOR, 1967). The coefficient b represents the degree of aggregation. These values for the different species calculated on monthly Tullgren cores over 16 months can be arranged in a definite sequence namely: *Isotomurus* (b = 1.60), with the highest aggregation; followed by *Lepidocyrtus* (b = 1.48), *Tomocerus* (b = 1.45), *Entomobrya* (b = 1.44) and *Orchesella* (b = 1.35) with the lowest aggregation.

A comparison of the degree of aggregation and locomotory activity in the field is made in Table II, where the periodical aggregation is given as a departure from the mean aggregation.

TABLE II

Degree of aggregation and locomotory activity during summer and winter

	Departure from mean aggregation		Mean activity (from pitfall catches)	
	winter	summer	winter	summer
Tomocerus minor	+ 0.13	— 0.04	7.8	19.1
Lepidocyrtus cyaneus	+ 0.34	— 0.11	4.3	24.5
Orchesella cincta	+ 0.21	— 0.07	9.7	36.3
Entomobrya nivalis	+ 0.40	— 0.12	8.1	19.6
Isotomurus palustris	— 0.04	+ 0.01	2.0	9.1
Isotoma viridis	— 0.12	+ 0.04	0.5	3.7

It can be concluded that in most species during winter, when aggregation is high, locomotory activity is low. Thus there seems to be an inverse relationship between locomotory activity and the degree of aggregation.

4. **Activity phenomena in the field**

Locomotory activity data were derived from catches in pitfall traps, which were corrected for the fluctuating density during the catching period of 64 weeks. The activity appeared to be variable, showing definite peaks especially in spring and autumn. The mean activity level of the species studied, apart from the peaks, showed differences (Table III).

TABLE III

Mean activity level in the field and relation between activity and temperature

	Mean act. level (without peaks)	Temp. (°C)				
		— 10/— 5	— 5/0	0/5	5/10	10/15
loc. act. of						
Tomocerus minor	2.4	1.9	1.6	2.4	6.7	10.5
Lepidocyrtus cyaneus.	3.7	1.8	2.6	8.6	12.8	4.3
Orchesella cincta	4.4	0.6	1.7	6.0	14.5	8.0
Entomobrya nivalis ..	2.7	1.7	1.8	2.8	11.4	4.2
Isotoma viridis	1.0	0	0.5	0.5	3.4	3.8
Isotomutus palustris ..	1.9	0.3	0.5	3.1	11.1	15.2

It is remarkable that the species with the highest humidity requirements are the least active.

The relation between the locomotory activity and the temperature during the catching periods (Table III) suggests, that species with high humidity requirements are more active in higher temperatures. This can be explained by the fact that in the soil in general higher temperatures correspond with higher s.d. values, for which these species are very sensitive in their locomotory activity reactions.

5. **Activity and reproduction**

Investigations were started to study any possible relation between locomotory activity and reproduction. A hundred individuals of *Orchesella cincta* and of *Tomocerus minor* respectively, which were synchronized in their reproduction, were observed in the laboratory in their egg-laying and feeding-habits.

In Fig. 3 the course of the activity (% of active animals) during 2 moulting intervals is given. During ecdysis a very low activity can be noticed. It is further evident that a definite rythm can be noticed in successive moults, consisting of an alternating egg-laying (spermatophora depositing) interval and a rest-interval. The reproductive phase is characterized by higher locomotory activity; the animals move around on the bottoms of the culture jars in search for places where eggs or spermatophores can be deposited. Since in this phase the percentage of animals present on the food is very low, feeding seems hardly to take place. The rest-phase is characterized by lower activity, the animals mostly being clumped together on their food substances (Fig. 3). This pattern is obvious both in *Orchesella* and in *Tomocerus,* but there seems to be a marked difference in the amount of activity in the reproductive phases, *Orchesella* being much more active.

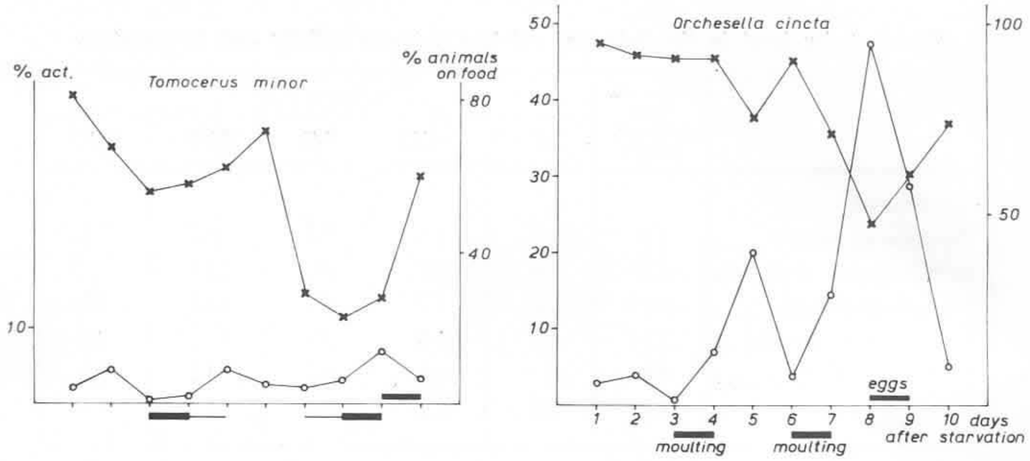

FIG. 3. — Course of locomotory activity of Collembola during a reproductive and a feeding phase. ×' —— × % animals on food; o —— o % active.

Locomotory activity in ♀ in relation to searching for spermatophores could not be demonstrated. While a concentration of 100 sperm packets was offered to females of *Orchesella cincta,* they did not show any reactions except at distances below 2 mm.

DISCUSSION

The previous experiments show that a relation exists between the humidity requirements of the collembolan species and their distribution and locomotory activity in the field. Species with high humidity requirements are forced in aggregations and show therefore a lower general activity level in the field. This general activity level appears to be determined by the temperature-s.d. conditions.

This survival mechanism, by which the animals are forced into aggregations may play an important role in increasing the meeting chance between individuals in a population, which may be important in reproduction. If this is the case, one could expect that species with lower aggregational habits should need other mechanisms to bring the individuals together. A remarkable phenomenon can be stressed in this respect: « lower » species, which in general have little resistance to desiccation and a high degree of aggregation (POOLE, 1964) do not show any courtship behaviour (MAYER, 1957). The « higher » species, which are more free in their movements show different degrees of reproductive behaviour. From the present specific difference in activity during egg-laying were obvious study. It seems that in Collembola this development is associated with the aggregational habits caused by humidity requirements.

Further investigation may show the character of this relation, which may contribute to the knowledge of ecological development in Collembola.

SUMMARY

An investigation was made in laboratory and field on the relation between humidity requirements of surface dwelling Collembola and their locomotory activity and aggregational habits.

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